

# ROTATING WAVES IN THE THETA MODEL FOR A RING OF SYNAPTICALLY CONNECTED NEURONS

GUY KATRIEL

**ABSTRACT.** We study rotating waves in the Theta model for a ring of synaptically-interacting neurons. We prove that when the neurons are oscillatory, at least one rotating wave always exists. In the case of excitable neurons, we prove that no travelling waves exist when the synaptic coupling is weak, and at least two rotating waves, a ‘fast’ one and a ‘slow’ one, exist when the synaptic coupling is sufficiently strong. We derive explicit upper and lower bounds for the ‘critical’ coupling strength as well as for the wave velocities. We also study the special case of uniform coupling, for which complete analytical results on the rotating waves can be achieved.

## 1. INTRODUCTION

In this work we study rotating waves in rings of neurons described by the Theta model. The Theta model [2, 3, 5, 6], which is derived as a canonical model for neurons near a ‘saddle-node on a limit cycle’ bifurcation, assumes the state of the neuron is given by an angle  $\theta$ , with  $\theta = (2l + 1)\pi$ ,  $l \in \mathbb{Z}$  corresponding to the ‘firing’ state, and the dynamics described by

$$(1) \quad \frac{d\theta}{dt} = 1 - \cos(\theta) + (1 + \cos(\theta))(\beta + I(t)),$$

where  $I(t)$  represents the inputs to the neuron. When  $\beta < 0$  this represents an ‘excitable’ neuron, which in the absence of external input ( $I \equiv 0$ ) approaches a rest state, while if  $\beta > 0$  this represents an ‘oscillatory’ neuron which performs spontaneous oscillations in the absence of external input.

A model of synaptically connected neurons on a continuous spacial domain  $\Omega$  takes the form:

$$(2) \quad \frac{\partial \theta(x, t)}{\partial t} = 1 - \cos(\theta(x, t)) + (1 + \cos(\theta(x, t))) \left[ \beta + g \int_{\Omega} J(x - y) s(y, t) dy \right],$$

$$(3) \quad \frac{\partial s(x, t)}{\partial t} + s(x, t) = P(\theta(x, t))(1 - cs(x, t)),$$

---

Partially supported by the Edmund Landau Center for Research in Mathematical Analysis and Related Areas, sponsored by the Minerva Foundation (Germany).

where  $J$  is a positive function and  $P$  is defined by

$$(4) \quad P(\theta) = \sum_{l=-\infty}^{\infty} \delta(\theta - (2l+1)\pi).$$

Here  $s(x, t)$  ( $x \in \Omega, t \in \mathbb{R}$ ) measures the synaptic transmission from the neuron located at  $x$ , and according to (3),(4) it decays exponentially, except when the neuron fires (*i.e.* when  $\theta(x, t) = (2l+1)\pi$ ,  $l \in \mathbb{Z}$ ), when it experiences a jump. (2) says that the neurons are modelled as Theta-neurons, where the input  $I(x, t)$  to the neuron at  $x$ , as in (1), is given by

$$I(x, t) = g \int_{\Omega} J(x-y)s(y, t)dy.$$

$J(x-y)$  (here assumed to be positive) describes the relative strength of the synaptic coupling from the neuron at  $x$  to the neuron at  $y$ , while  $g > 0$  is a parameter measuring the overall coupling strength.

The above model, in the case  $c > 0$ , is the one presented in [2, 7]. In the case  $c = 0$  this model is the one presented in [6] (Remark 2) and [9]. We always assume  $c \geq 0$ .

When the geometry is linear,  $\Omega = \mathbb{R}$ , it is natural to seek travelling waves of activity along the line in which each neuron makes one or more oscillations and then approaches rest. In [8] it was proven that for sufficiently strong synaptic coupling  $g$ , at least two such waves, a slow and a fast one, exist, and also that they always involve each neuron firing more than one time before it approaches rest, while for sufficiently small  $g$  such waves do not exist. It was not determined how many times each neuron fires before coming to rest, and it may even be that each neuron fires infinitely many times. Some numerical results in the case of a one and a two-dimensional geometry were obtained in [7].

In this work we consider a different possibility for the spacial geometry:  $\Omega = S^1$ , so the neurons are placed on a ring and our equations are (3) and

$$(5) \quad \frac{\partial \theta(x, t)}{\partial t} = h(\theta(x, t)) + gw(\theta(x, t)) \int_{-\pi}^{\pi} J(x-y)s(y, t)dy.$$

with

$$(6) \quad h(\theta) = 1 - \cos(\theta) + \beta(1 + \cos(\theta)), \quad w(\theta) = 1 + \cos(\theta),$$

where  $J$  is continuous, positive and periodic

$$(7) \quad J(x) > 0 \quad \forall x \in \mathbb{R},$$

$$(8) \quad J(x + 2\pi) = J(x) \quad \forall x \in \mathbb{R},$$

and the solutions satisfy the periodicity conditions

$$(9) \quad \theta(x + 2\pi, t) = \theta(x, t) + 2\pi m \quad \forall x, t \in \mathbb{R}$$

$$(10) \quad s(x + 2\pi, t) = s(x, t) \quad \forall x, t \in \mathbb{R}$$

The integer  $m$  (the ‘winding number’) is determined by the initial condition  $\theta(x, 0)$ , and will be preserved as long as the solution remains continuous.

In this geometry, a different kind of wave of activity is possible: a wave that rotates around the ring repeatedly. Such waves, that is solutions of the form:

$$(11) \quad \theta(x, t) = \phi(x + vt)$$

$$(12) \quad s(x, t) = r(x + vt)$$

where  $v$  is the wave velocity, are the focus of our investigation.

In section 2 we show that in the case that the winding number  $m = 0$ , there can exist only trivial rotating waves. Thus the interesting cases are when  $m > 0$ . Here we study the case  $m = 1$ , the case  $m > 1$  being beyond our reach. Thus, this work concentrates on the first non-trivial case.

Our central results about existence, nonexistence and multiplicity of rotating waves can be summarized as follows (see figures 1,2 for the *simplest* diagrams consistent with these results):

**Theorem 1.** *Consider the equations (5),(3) with conditions (9), (10), and  $m = 1$ .*

(I) *In the oscillatory case  $\beta > 0$ : for all  $g > 0$  there exists a rotating wave, with velocity going to  $+\infty$  as  $g \rightarrow +\infty$ .*

(II) *In the excitable case  $\beta < 0$ :*

(i) *For  $g > 0$  sufficiently small there exist no rotating waves.*

(ii) *for  $g$  sufficiently large there exist at least two rotating waves, a ‘fast’ and a ‘slow’ one, in the sense that their velocities approach  $+\infty$  and 0, respectively, as  $g \rightarrow +\infty$ .*

Therefore our results bear resemblance to those obtained in [8] for the case of a linear geometry. We note that although for the rotating waves found here each neuron fires infinitely many times, the reason for this is that it is re-excited each time, because of the periodic geometry. During each revolution of the rotating wave, each neuron fires once, so naively one could think that the analogous phenomenon in a linear geometry would be a travelling wave with each neuron firing once - but this was shown to be impossible in [8]. It is interesting to note that while in [8] some restrictions were made on the coupling function  $J$ , like being decreasing with distance, here no such restrictions are imposed beyond (7), (8). We would expect however that some restriction would need to be imposed on  $J$  in order to obtain stability of travelling waves. The whole issue of stability remains quite open and awaits future investigation. In the case  $\Omega = \mathbb{R}$ , both numerical evidence in [7, 8]

and results obtained in other models [1] indicate that the fast wave is stable while the slow wave is unstable, so we might conjecture that this is true for the case investigated here as well - at least under some natural assumptions on  $J$ . Some analytical progress on the stability question in the case  $\Omega = \mathbb{R}$  has recently been achieved in [9].

Let us note that the model considered here, in the case  $\beta < 0$ , describes waves in an excitable medium, about which an extensive literature exists (see [10] and references therein). However, most models consider diffusive rather than synaptic coupling. In the case of the Theta model on a ring, with *diffusive* coupling, and  $m = 1$ , it is proven in [4] that a rotating wave exists regardless of the strength of coupling (*i.e.* the diffusion coefficient), so that our results highlight the difference between diffusive and synaptic coupling.

In section 3 we reduce the study of rotating waves to the investigation of the zeroes of a function of one variable. In section 4 we investigate the special case in which the coupling is uniform ( $J(x)$  is a constant function), which, although artificial from a biological point of view, allows us to obtain closed analytic expressions for the wave-velocity vs. coupling-strength curves in an elementary fashion. We can thus gain some intuition for the general case, and obtain information which is unavailable in the case of general  $J$ , like precise multiplicity results. It is interesting to investigate to what extent the more precise results obtained in the uniform-coupling case extend to the general case, and we shall indicate several questions, which remain open, in this direction. In section 5 we turn to the case of general coupling functions  $J$ , and prove the results of theorem 1 above, obtaining also some quantitative estimates: lower and upper bounds for the critical values of synaptic coupling coupling strength  $g$ , as well as for the wave velocities.

## 2. PRELIMINARIES

We begin with an elementary calculus lemma which is useful in several of our arguments below.

**Lemma 2.** *Let  $f : \mathbb{R} \rightarrow \mathbb{R}$  be a differentiable function, and let  $b, c \in \mathbb{R}$ ,  $b \neq 0$ , be constants such that we have the following property:*

$$(13) \quad f(z) = c \Rightarrow f'(z) = b.$$

*Then the equation  $f(z) = c$  has at most one solution.*

PROOF: Assume by way of contradiction that the equation  $f(z) = c$  has at least two solutions  $z_0 < z_1$ . Define  $S \subset \mathbb{R}$  by

$$S = \{z > z_0 \mid f(z) = c\}.$$

$S$  is nonempty because  $z_1 \in S$ . Let  $\underline{z} = \inf S$ . By continuity of  $f$  we have  $f(\underline{z}) = c$ . We have either  $\underline{z} > z_0$  or  $\underline{z} = z_0$ , and we shall show that both of

these possibilities lead to contradictions. If  $\underline{z} > z_0$ , then by (13) we have

$$f(z_0) = f(\underline{z}) = c$$

$$\text{sign}(f'(z_0)) = \text{sign}(f'(\underline{z})) = \text{sign}(b)$$

so we conclude that there exists  $z_2 \in (z_0, \underline{z})$  with  $f(z_2) = c$ , contradicting the definition of  $\underline{z}$ . If  $\underline{z} = z_0$  then  $z_0$  is a limit-point of  $S$ , which implies that  $f'(z_0) = 0$ , contradicting (13). These contradictions conclude our proof.

Turning now to our investigation, we note a few properties of the functions  $h(\theta)$  and  $w(\theta)$  defined by (6) which will be used often in our arguments:

$$(14) \quad h((2l+1)\pi) = 2 \quad \forall l \in \mathbb{Z},$$

$$(15) \quad h(2l\pi) = 2\beta, \quad \forall l \in \mathbb{Z},$$

$$(16) \quad w((2l+1)\pi) = 0 \quad \forall l \in \mathbb{Z},$$

$$(17) \quad w(2l\pi) = 2 \quad \forall l \in \mathbb{Z},$$

Plugging (11),(12) into (5), (3), and setting  $z = x + vt$  we obtain the following equations for  $\phi(z)$ ,  $r(z)$ :

$$(18) \quad v\phi'(z) = h(\phi(z)) + gw(\phi(z)) \int_{-\pi}^{\pi} J(z-y)r(y)dy,$$

$$(19) \quad vr'(z) + r(z) = P(\phi(z))(1 - cr(z)).$$

In order to satisfy the boundary conditions (9),(10),  $\phi$  and  $r$  have to satisfy

$$(20) \quad \phi(z + 2\pi) = \phi(z) + 2\pi m \quad \forall z \in \mathbb{R},$$

$$(21) \quad r(z + 2\pi) = r(z) \quad \forall z \in \mathbb{R}.$$

Let us first dispose of the case of zero-velocity waves,  $v = 0$ . We get the equations

$$(22) \quad h(\phi(z)) + gw(\phi(z)) \int_{-\pi}^{\pi} J(z-y)r(y)dy = 0,$$

$$(23) \quad r(z) = P(\phi(z))(1 - cr(z)).$$

If there exists some  $z_0 \in \mathbb{R}$  with  $\phi(z_0) = (2l+1)\pi$ ,  $l \in \mathbb{Z}$ , then, substituting  $z = z_0$  into (22) and using (14),(16), we obtain  $2 = 0$ , a contradiction. Hence we must have

$$(24) \quad \phi(z) \neq (2l+1)\pi \quad \forall z \in \mathbb{R}, \quad l \in \mathbb{Z}$$

which implies that  $P(\phi(z)) \equiv 0$ , so that (23) gives  $r(z) \equiv 0$ , and (22) reduces to  $h(\phi(z)) \equiv 0$ , and thus  $\phi(z)$  is a constant function, the constant being a root of  $h(\theta)$ . This implies, first of all, that the winding number  $m$  is 0, since a constant  $\phi(z)$  cannot satisfy (20) otherwise. In addition the function  $h(\theta)$  must vanish somewhere, which is equivalent to the condition  $\beta \leq 0$ . We have thus proven

**Lemma 3.** *Zero-velocity waves exist if and only if  $m = 0$  and  $\beta \leq 0$ , and in this case they are just the stationary solutions*

$$r(z) \equiv 0$$

$$\phi(z) \equiv \pm \cos^{-1} \left( \frac{\beta + 1}{\beta - 1} \right) + 2\pi k, \quad k \in \mathbb{Z}.$$

We will now show that the trivial “waves” of lemma 3 are the only ones that occur for  $m = 0$ .

**Lemma 4.** *Assume  $m = 0$ .*

(i) *If  $\beta > 0$  there are no rotating waves.*

(ii) *If  $\beta \leq 0$  the only rotating waves are those given by lemma 3.*

PROOF: Assume  $(v, \phi(z), r(z))$  is a solution of (18),(19) satisfying (20) with  $m = 0$ , i.e.

$$(25) \quad \phi(z + 2\pi) = \phi(z) \quad \forall z \in \mathbb{R},$$

and (21). We also assume  $v \neq 0$ , otherwise we are back to lemma 3. We shall prove below that  $\phi(z)$  must satisfy (24), and hence that  $P(\phi(z)) \equiv 0$ , so that by (19),(21) we have  $r(z) \equiv 0$ , so that (18) reduces to

$$(26) \quad v\phi'(z) = h(\phi(z)).$$

Since  $v \neq 0$ , if  $h(\theta)$  has no roots ( $\beta > 0$ ), (26) has no solutions satisfying (25). If  $h(\theta)$  does have roots ( $\beta \leq 0$ ) then the only solutions of (26) satisfying (25) are constant functions, the constant being a root of  $h(\theta)$ , and we are back to the same solutions given in lemma 3, which indeed can be considered as rotating waves with arbitrary velocity.

It remains then to prove that (24) must hold. Assume by way of contradiction that  $\phi(z_0) = (2l + 1)\pi$  for some integer  $l$ . By (14),(16),(18), and the assumption  $v \neq 0$ , we have

$$\phi(z) = (2l + 1)\pi \Rightarrow \phi'(z) = \frac{2}{v}.$$

Thus the assumptions of lemma 2, with  $f = \phi$ ,  $c = (2l + 1)\pi$ ,  $b = \frac{2}{v}$ , are satisfied, and we conclude that the equation  $\phi(z) = (2l + 1)\pi$  has at most one solution, contradicting the fact that, by (25), we have  $\phi(z_0) = \phi(z_0 + 2\pi) = (2l + 1)\pi$ .

Having found all possible rotating waves in the case  $m = 0$ , we can now turn to the case  $m > 0$ . In fact, as was mentioned in the introduction, we shall treat the case  $m = 1$ , the cases  $m > 1$  being harder. By lemma 3 we know that there are no zero-velocity waves, so we can assume  $v \neq 0$  and define

$$(27) \quad \lambda = \frac{1}{v},$$

so that our equations for the rotating waves can be rewritten

$$(28) \quad \phi'(z) = \lambda h(\phi(z)) + \lambda g w(\phi(z)) \int_{-\pi}^{\pi} J(z-y) r(y) dy,$$

$$(29) \quad r'(z) + \lambda r(z) = \lambda P(\phi(z))(1 - cr(z)),$$

with periodic conditions

$$(30) \quad \phi(z + 2\pi) = \phi(z) + 2\pi \quad \forall z \in \mathbb{R},$$

$$(31) \quad r(z + 2\pi) = r(z) \quad \forall z \in \mathbb{R}.$$

### 3. REDUCTION TO A ONE-DIMENSIONAL EQUATION

We study the equations (28),(29) for  $(\lambda, \phi(z), r(z))$  with periodic conditions (30),(31). We will derive a scalar equation (see (52) below) so that rotating waves are in one-to-one correspondence with solutions of that equation.

We note first that, since by (31) we have  $\phi(\mathbb{R}) = \mathbb{R}$ , and since any rotating wave generates a family of other rotating waves by translations, we may, without loss of generality, fix

$$(32) \quad \phi(0) = \pi.$$

The following lemma shows that for a rotating wave (in the case  $m = 1$ ) there is at any specific time a unique neuron on the ring which is firing. This fact is very important for our analysis.

**Lemma 5.** *Assume  $(\lambda, \phi, r)$  satisfy (28),(29) with conditions (30),(31),(32). Then*

$$(33) \quad z \in (0, 2\pi) \Rightarrow \pi < \phi(z) < 3\pi$$

$$(34) \quad z \in (-2\pi, 0) \Rightarrow -\pi < \phi(z) < \pi$$

PROOF: (34) follows from (33) by (30). To prove (33), we first note that certainly  $\lambda \neq 0$ , since  $\lambda = 0$  and (28) imply  $\phi(z)$  is constant, contradicting (30).

We note the key fact that, by (28),(14) and (16),

$$(35) \quad \phi(z) = (2l + 1)\pi, \quad l \in \mathbb{Z} \quad \Rightarrow \quad \phi'(z) = 2\lambda.$$

By lemma 2, (35) implies that the equation  $\phi(z) = 2l + 1$  has at most one solution for each  $l \in \mathbb{Z}$ . In particular, since  $\phi(0) = \pi$ ,  $\phi(2\pi) = 3\pi$  we have  $\phi(z) \neq \pi, 3\pi$  for  $z \in (0, 2\pi)$ , and by continuity of  $\phi(z)$  this implies (33).

Let us note that if we knew that for rotating waves the function  $\phi(z)$  must be monotone, then lemma 5 would follow immediately from (32).

*Question 6.* Is it true in general that rotating wave solutions are monotone (for  $m_0$ )?

**Lemma 7.** *Assume  $(\lambda, \phi, r)$  satisfy (28), (29) with conditions (30), (31), (32). Then  $\lambda > 0$ .*

In other words,  $v > 0$  for all rotating waves with  $m = 1$ , so the waves rotate clockwise. Of course in the symmetric case  $m = -1$  the waves will rotate counter-clockwise.

PROOF: By (32) and (35) we have  $\phi'(0) = 2\lambda$ . We have already noted that  $\lambda \neq 0$ . If  $\lambda$  were negative, then  $\phi$  would be decreasing near  $z = 0$ , so for small  $z > 0$  we would have  $\phi(z) < 0$ , contradicting (33).

Our next step is to solve (29), (31) for  $r(z)$ , in terms of  $\phi(z)$ . We will use the following important consequence of lemma 5:

**Lemma 8.**

$$P(\phi(z))|_{(-2\pi, 2\pi)} = \frac{1}{2\lambda} \delta(z)$$

PROOF: By lemma 5 we have

$$P(\phi(z))|_{(-2\pi, 2\pi)} = \delta(\phi(z) - \pi),$$

so we will show that

$$(36) \quad \delta(\phi(z) - \pi) = \frac{1}{2\lambda} \delta(z).$$

Let  $\chi(z) \in C_0^\infty(\mathbb{R})$  be a test function. Using lemma 5 again we have

$$(37) \quad \int_{-\pi}^{\pi} \chi(u) \delta(\phi(u) - \pi) du = \int_{-\epsilon}^{\epsilon} \chi(u) \delta(\phi(u) - \pi) du,$$

where  $\epsilon > 0$  is arbitrary. In particular, since  $\phi'(0) = 2\lambda > 0$ , we may choose  $\epsilon > 0$  sufficiently small so that  $\phi'(z) > 0$  for  $z \in (-\epsilon, \epsilon)$ , so that we can make a change of variables  $\varphi = \phi(u)$ , obtaining

$$(38) \quad \begin{aligned} \int_{-\epsilon}^{\epsilon} \chi(u) \delta(\phi(u) - \pi) du &= \int_{\phi(-\epsilon)}^{\phi(\epsilon)} \chi(\phi^{-1}(\varphi)) \delta(\varphi - \pi) \frac{d\varphi}{\phi'(\phi^{-1}(\varphi))} \\ &= \frac{\chi(0)}{\phi'(\phi^{-1}(\pi))} = \frac{\chi(0)}{\phi'(0)} = \frac{\chi(0)}{2\lambda}. \end{aligned}$$



This proves (36), completing the proof of the lemma.

By lemma 8 we can rewrite equation (29) on the interval  $(-2\pi, 2\pi)$  as

$$(39) \quad r'(z) + \left(\lambda + \frac{c}{2}\delta(z)\right)r(z) = \frac{1}{2}\delta(z),$$

The solution of which is given by

$$(40) \quad r(z) = \left(\frac{1}{2}H(z) + r(-\pi)e^{-\pi\lambda}\right)e^{-(\lambda z + \frac{c}{2}H(z))},$$

where  $H$  is the Heaviside function:  $H(z) = 0$  for  $z < 0$ ,  $H(z) = 1$  for  $z > 0$ . Substituting  $z = \pi$  into (40) and using (31), we obtain an equation for  $r(-\pi)$  whose solution is

$$r(-\pi) = \frac{1}{2}(e^{\pi\lambda + \frac{c}{2}} - e^{-\pi\lambda})^{-1},$$

and substituting this back into (40), we obtain that the solution of (29),(31) which we denote by  $r_\lambda(z)$  in order to emphasize the dependence on the parameter  $\lambda$ , is given on the interval  $(-2\pi, 2\pi)$  by

$$(41) \quad r_\lambda(z) = \frac{1}{2}e^{-(\lambda z + \frac{c}{2}H(z))} \left[ H(z) + (e^{2\pi\lambda + \frac{c}{2}} - 1)^{-1} \right] \quad 0 < |z| < 2\pi.$$

We note that, for general  $z \in \mathbb{R}$ ,  $r_\lambda(z)$  is given as the  $2\pi$ -periodic extension of the function defined by (41) from  $[-\pi, \pi]$  to the whole real line.

The following result, which can be computed from (41), will be needed later

$$(42) \quad \int_{-\pi}^{\pi} r_\lambda(u) du = \frac{1}{2\lambda} \rho_c(\lambda),$$

where

$$\rho_c(\lambda) = \frac{e^{2\pi\lambda} - 1}{e^{2\pi\lambda + \frac{c}{2}} - 1}.$$

We note that

$$(43) \quad \rho_0(\lambda) \equiv 1,$$

A fact that considerably simplifies the formulas in the case  $c = 0$ .

The rotating waves correspond to solutions  $(\lambda, \phi)$  of the equation

$$(44) \quad \phi'(z) = \lambda h(\phi(z)) + \lambda g w(\phi(z)) \int_{-\pi}^{\pi} J(z-y) r_\lambda(y) dy,$$

with  $\phi(z)$  satisfying (32) and

$$(45) \quad \phi(\pi) = \phi(-\pi) + 2\pi.$$

To simplify notation, we define

$$(46) \quad R_\lambda(z) = \int_{-\pi}^{\pi} J(z-y) r_\lambda(y) dy,$$

so that (44) is rewritten as

$$(47) \quad \phi'(z) = \lambda h(\phi(z)) + \lambda g R_\lambda(z) w(\phi(z)).$$

We note that (47) is a nonautonomous differential equation for  $\phi(z)$ , and since the nonlinearities are bounded and Lipschitzian, the initial value problem (47),(32) has a unique solution, which we denote by  $\phi_\lambda$ .

Rotating waves thus correspond to solutions  $\lambda > 0$  of the equation

$$(48) \quad \phi_\lambda(\pi) - \phi_\lambda(-\pi) = 2\pi.$$

Rewriting (47) and (50) we have

$$(49) \quad \phi'_\lambda(z) = \lambda h(\phi_\lambda(z)) + \lambda g R_\lambda(z) w(\phi_\lambda(z)),$$

$$(50) \quad \phi_\lambda(0) = \pi,$$

and defining

$$(51) \quad \Psi(\lambda) = \frac{1}{2\pi}(\phi_\lambda(\pi) - \phi_\lambda(-\pi)),$$

we obtain that rotating waves correspond to solutions  $\lambda > 0$  of the equation

$$(52) \quad \Psi(\lambda) = 1.$$

#### 4. THE CASE OF UNIFORM COUPLING

Assuming that the coupling is  $J \equiv 1$  we shall be able to solve for the rotating waves explicitly. In this case we have, from (46),(42)

$$R_\lambda(z) = \int_{-\pi}^{\pi} r_\lambda(y) dy = \frac{1}{2\lambda} \rho_c(\lambda),$$

so that (49) reduces to

$$(53) \quad \phi'_\lambda(z) = \lambda h(\phi_\lambda(z)) + \frac{g}{2} \rho_c(\lambda) w(\phi_\lambda(z)).$$

The fact that (53) is an autonomous equation is what makes the treatment of the case  $J$  constant much simpler. Indeed, assume that (52) holds, so that

$$(54) \quad \phi_\lambda(\pi) - \phi_\lambda(-\pi) = 2\pi.$$

Then we have, using (53), making a change of variables  $\varphi = \phi_\lambda(z)$ , and using (54)

$$(55) \quad \begin{aligned} 1 &= \frac{1}{2\pi} \int_{-\pi}^{\pi} \frac{\phi'(z) dz}{\lambda h(\phi(z)) + \frac{g}{2} \rho_c(\lambda) w(\phi(z))} \\ &= \frac{1}{2\pi} \int_{\phi_\lambda(-\pi)}^{\phi_\lambda(\pi)} \frac{d\varphi}{\lambda h(\varphi) + \frac{g}{2} \rho_c(\lambda) w(\varphi)} = \frac{1}{2\pi} \int_{-\pi}^{\pi} \frac{d\varphi}{\lambda h(\varphi) + \frac{g}{2} \rho_c(\lambda) w(\varphi)}. \end{aligned}$$

Substituting the explicit expressions for  $h$  and  $w$  from (6), and using the formula

$$(56) \quad \frac{1}{2\pi} \int_{-\pi}^{\pi} \frac{d\phi}{A + B\cos(\phi)} = \frac{1}{\sqrt{A^2 - B^2}} \quad (|A| > |B|),$$

(55) becomes

$$(57) \quad 1 = \frac{1}{\sqrt{4\lambda^2\beta + 2g\lambda\rho_c(\lambda)}},$$

so that rotating waves correspond to solutions of (57), with their velocities given by  $v = \frac{1}{\lambda}$ . We can rewrite (57) as

$$(58) \quad f_{c,\beta}(\lambda) = g, \quad \lambda > 0$$

where

$$(59) \quad f_{c,\beta}(\lambda) = \frac{1 - 4\beta\lambda^2}{2\lambda\rho_c(\lambda)}.$$

In the following lemma we collect some properties of the functions  $f_{c,\beta}(\lambda)$ , which are obtained by elementary calculus:

**Lemma 9.** (i) When  $\beta < 0$ ,  $f_{c,\beta}$  is positive and convex on  $(0, \infty)$ , and

$$(60) \quad \lim_{\lambda \rightarrow 0} f_{c,\beta}(\lambda) = \infty,$$

$$(61) \quad \lim_{\lambda \rightarrow \infty} f_{c,\beta}(\lambda) = \infty.$$

(ii) When  $\beta \geq 0$ ,  $f_{c,\beta}$  is decreasing on  $(0, \infty)$ , and (60) holds. If  $\beta > 0$  it has a zero at  $\lambda = \frac{1}{2\sqrt{\beta}}$ , if  $\beta = 0$  it is positive on  $(0, \infty)$  and  $\lim_{\lambda \rightarrow \infty} f_{c,0}(\lambda) = 0$ .

From lemma 9 we conclude that when  $\beta < 0$  (58) has exactly two solutions if  $g > \Omega(c, \beta)$ , where

$$(62) \quad \Omega(c, \beta) = \min_{\lambda > 0} f_{c,\beta}(\lambda),$$

which we will denote by

$$\Delta_{c,\beta}(g) < \bar{\lambda}_{c,\beta}(g),$$

no solution if  $g < \Omega(c, \beta)$ , and a unique solution when  $g = \Omega(c, \beta)$ .

When  $\beta \geq 0$ , part (ii) of lemma 9 implies that (58) has a unique solution for any  $g > 0$ , which we denote by  $\lambda_{c,\beta}(g)$ .

An elementary asymptotic analysis of the equation (58) yields

**Lemma 10.** (i) When  $\beta < 0$  we have the following asymptotics as  $g \rightarrow \infty$

$$(63) \quad \bar{\lambda}_{c,\beta}(g) = \frac{e^{-\frac{g}{2}}}{2|\beta|} g + O\left(\frac{1}{g}\right) \quad \text{as } g \rightarrow \infty.$$

For  $\underline{\lambda}_{c,\beta}(g)$ , in case  $c > 0$  we have

$$(64) \quad \underline{\lambda}_{c,\beta}(g) = \frac{1}{2} \sqrt{\frac{1}{\pi}(e^{\frac{\pi}{2}} - 1)} \frac{1}{\sqrt{g}} + O\left(\frac{1}{g}\right) \quad \text{as } g \rightarrow \infty,$$

while in case  $c = 0$  we have

$$(65) \quad \underline{\lambda}_{0,\beta}(g) = \frac{1}{2} \frac{1}{g} + O\left(\frac{1}{g^2}\right) \quad \text{as } g \rightarrow \infty.$$

(ii) For  $\beta \geq 0$ , the asymptotics of  $\lambda_{c,\beta}(g)$  as  $g \rightarrow \infty$  are the same as those of  $\underline{\lambda}_{c,\beta}(g)$ , given in (64) for  $c > 0$  and (65) for  $c = 0$ .

We thus obtain

**Theorem 11.** When  $J \equiv 1$ :

(I) In the excitable case  $\beta < 0$ :

(i) If  $g > \Omega(g, c)$  there exist two rotating waves with velocities given by

$$(66) \quad \underline{v}_{c,\beta}(g) = \frac{1}{\underline{\lambda}_{c,\beta}(g)}, \quad \overline{v}_{c,\beta}(g) = \frac{1}{\overline{\lambda}_{c,\beta}(g)},$$

and we have, for the slow wave

$$(67) \quad \underline{v}_{c,\beta}(g) = 2|\beta|e^{\frac{\pi}{2}} \frac{1}{g} + O\left(\frac{1}{g^3}\right) \quad \text{as } g \rightarrow \infty,$$

for the fast wave when  $c > 0$ :

$$(68) \quad \overline{v}_{c,\beta}(g) = 2\sqrt{\frac{\pi}{e^{\frac{\pi}{2}} - 1}} \sqrt{g} + O(1) \quad \text{as } g \rightarrow \infty.$$

while for the fast wave when  $c = 0$

$$(69) \quad \overline{v}_{0,\beta}(g) = 2g + O\left(\frac{1}{g}\right) \quad \text{as } g \rightarrow \infty.$$

(ii) If  $g = \Omega(c, \beta)$  there exists a unique rotating wave with velocity

$$(70) \quad v = \underline{v}_{c,\beta}(g) = \overline{v}_{c,\beta}(g).$$

(iii) If  $g < \Omega(c, \beta)$  there exist no rotating waves.

(II) When  $\beta \geq 0$ , there exists a unique rotating wave for any  $g > 0$ , whose velocity is given by

$$(71) \quad v_{c,\beta}(g) = \frac{1}{\lambda_{c,\beta}(g)},$$

and for large  $g$  it has the same asymptotics as in (68), (69) in the cases  $c > 0$ ,  $c = 0$ , respectively.

In the excitable case we thus have two rotating waves born at a supercritical saddle-node bifurcation as the coupling strength  $g$  crosses  $\Omega(c, \beta)$ .

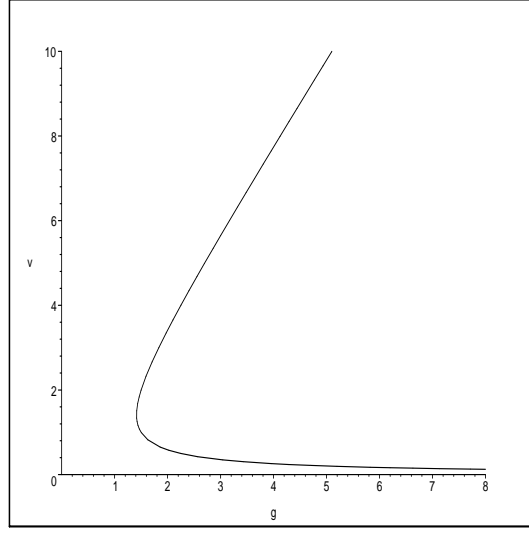


FIGURE 1. Velocity of waves ( $v$ ) vs. coupling strength ( $g$ ) for the case  $J \equiv 1$ ,  $c = 0$ ,  $\beta = -0.5$ .

We now note that in the special case  $c = 0$  (the model introduced in [6]) we can obtain more explicit expressions. Using (43) we have

$$f_{0,\beta}(\lambda) = \frac{1 - 4\beta\lambda^2}{2\lambda}.$$

The minimum in (62) can now be computed explicitly, and we obtain, when  $\beta < 0$ ,

$$\Omega(0, \beta) = 2\sqrt{|\beta|}.$$

We can also solve (58) explicitly, and obtain the velocities of the rotating waves. When  $\beta < 0$ ,  $g > \Omega(0, \beta)$

$$\underline{v}_{0,\beta}(g) = g - \sqrt{g^2 + 4\beta}, \quad \overline{v}_{0,\beta}(g) = g + \sqrt{g^2 + 4\beta}.$$

When  $\beta \geq 0$ , for all  $g > 0$

$$v_{0,\beta}(g) = \sqrt{g^2 + 4\beta} + g.$$

Figures 1,2 show the wave-velocity vs. coupling strength diagrams for the rotating waves when  $J \equiv 1$ ,  $c = 0$ , in an excitable ( $\beta = -0.5$ ) and an oscillatory ( $\beta = 0.5$ ) case. In figures 3,4 we change  $c$  to  $c = 1$ .

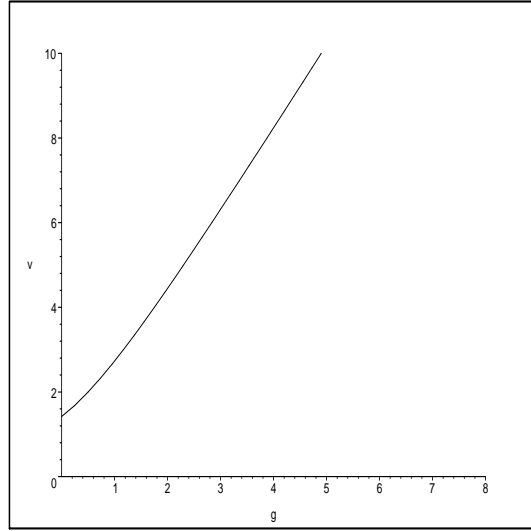


FIGURE 2. Velocity of waves ( $v$ ) vs. coupling strength ( $g$ ) for the case  $J \equiv 1$ ,  $c = 0$ ,  $\beta = 0.5$ .

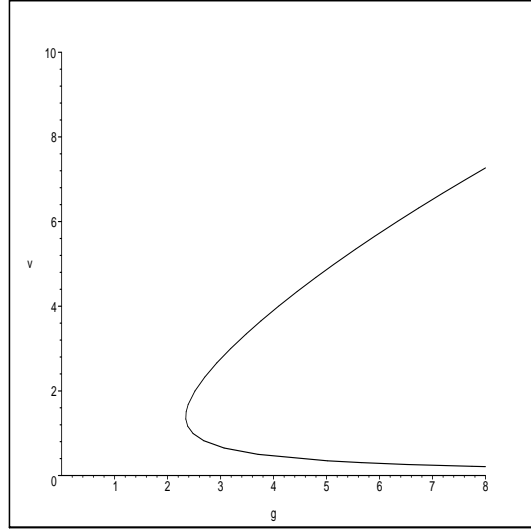


FIGURE 3. Velocity of waves ( $v$ ) vs. coupling strength ( $g$ ) for the case  $J \equiv 1$ ,  $c = 1$ ,  $\beta = -0.5$ .

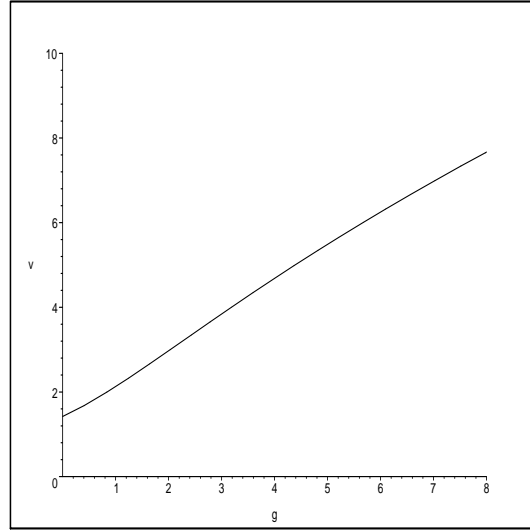


FIGURE 4. Velocity of waves ( $v$ ) vs. coupling strength ( $g$ ) for the case  $J \equiv 1$ ,  $c = 1$ ,  $\beta = 0.5$ .

## 5. THE GENERAL CASE

We now return to the case when  $J$  is a general continuous positive  $2\pi$ -periodic function, and prove that several of the results about rotating waves obtained above for the special case  $J \equiv 1$  remain valid, though the proofs are necessarily less direct.

**Lemma 12.**

$$\lim_{\lambda \rightarrow 0} \Psi(\lambda) = 0.$$

PROOF: We shall prove that

$$(72) \quad \phi_\lambda(z) = \pi + O(\lambda) \quad \text{as } \lambda \rightarrow 0$$

uniformly in  $z \in [-\pi, \pi]$ . The lemma follows immediately from this and from (51).

When  $c > 0$ , the claim (72) is immediate, since, using (41),

$$\lim_{\lambda \rightarrow 0} r_\lambda(z) = \frac{1}{2} e^{-\frac{c}{2} H(z)} \left[ (e^{\frac{c}{2}} - 1)^{-1} + H(z) \right], \quad 0 < |z| < 2\pi,$$

so that

$$(73) \quad \lambda R_\lambda(z) = O(\lambda) \quad \text{as } \lambda \rightarrow 0,$$

which implies that the right-hand side of (47) is  $O(\lambda)$ .

For  $c = 0$ ,  $r_\lambda(z)$  becomes singular as  $\lambda \rightarrow 0$ , so we need a more refined argument. For  $\lambda r_\lambda(z)$  we have

$$(74) \quad \lambda r_\lambda(z) = \frac{1}{4\pi} + O(\lambda) \quad \text{as } \lambda \rightarrow 0,$$

uniformly in  $z \in [-\pi, \pi]$ , hence

$$(75) \quad \lambda R_\lambda(z) = \frac{1}{2}\overline{J} + O(\lambda) \quad \text{as } \lambda \rightarrow 0,$$

where

$$\overline{J} = \frac{1}{2\pi} \int_{-\pi}^{\pi} J(x) dx.$$

The standard theorems on dependence of solutions of initial-value problems on parameters hence imply

$$\phi_\lambda(z) = \phi_0(z) + O(\lambda) \quad \text{as } \lambda \rightarrow 0,$$

uniformly in  $z \in [-\pi, \pi]$ , where  $\phi_0$  satisfies

$$(76) \quad \phi'_0(z) = \frac{g\overline{J}}{2} w(\phi_0(z))$$

and  $\phi_0(0) = \pi$ . Since, by (16), the constant function  $\pi$  is a solution to this initial-value problem, the uniqueness theorem for initial-value problems implies that  $\phi_0(z) \equiv \pi$ .

The following bounds, which follow immediately from (46) and (42), will be useful:

**Lemma 13.** (i) We have, for all  $z \in [-\pi, \pi]$ :

$$\frac{1}{2\lambda} \rho_c(\lambda) \min_{x \in \mathbb{R}} J(x) \leq R_\lambda(z) \leq \frac{1}{2\lambda} \rho_c(\lambda) \max_{x \in \mathbb{R}} J(x).$$

(ii) If  $J$  is not a constant function, the inequalities of (i) are strict.

**Lemma 14.** In the excitable case  $\beta < 0$ , we have

$$\frac{\lambda}{\rho_c(\lambda)} \geq \frac{g}{2|\beta|} \max_{x \in \mathbb{R}} J(x) \Rightarrow \Psi(\lambda) < 1,$$

PROOF: In the case of constant  $J$  the result can be proven by direct computation, so we now assume  $J$  is not a constant function. We will show that when

$$(77) \quad \frac{\lambda}{\rho_c(\lambda)} \geq \frac{g}{2|\beta|} \max_{x \in \mathbb{R}} J(x)$$

we have

$$(78) \quad \phi_\lambda(z) < 2\pi \quad \forall z \in [0, \pi],$$



$$(79) \quad \phi_\lambda(z) > 0 \quad \forall z \in [-\pi, 0].$$

Together with (51), these imply the result of our lemma. To prove our claim we note that, using (49),(15),(17), part (ii) of lemma 13 (which is why we need the assumption that  $J$  is non-constant) and (77)

$$(80) \quad \begin{aligned} \phi_\lambda(z) = 0 \text{ or } 2\pi &\Rightarrow \phi'_\lambda(z) = 2\lambda\beta + 2\lambda g R_\lambda(z) \\ &< 2\lambda\beta + g\rho_c(\lambda) \max_{x \in \mathbb{R}} J(x) \leq 2\lambda\beta + 2\lambda|\beta| = 0. \end{aligned}$$

We now show that (80) implies (78). If (78) fails to hold, then we set

$$z_0 = \min \{z \in [0, \pi] \mid \phi_\lambda(z) = 2\pi\}.$$

This number is well-defined by continuity and by the fact that  $\phi_\lambda(0) = \pi$ , which implies also that  $z_0 > 0$ . By (80) we have  $\phi'_\lambda(z_0) < 0$ , but this implies that  $\phi_\lambda(z)$  is decreasing in a neighborhood of  $z_0$ , and in particular that there exist  $z \in (0, z_0)$  satisfying  $\phi_\lambda(z) = 2\pi$ . But this contradicts the definition of  $z_0$ , and this contradiction proves (78). Similarly, assuming (79) does not hold and defining

$$z_1 = \max \{z \in [-\pi, 0] \mid \phi_\lambda(z) = 0\},$$

we conclude that  $z_1 < 0$  and  $\phi'_\lambda(z_1) < 0$ , so that  $\phi_\lambda(z)$  is decreasing in a neighborhood of  $z_1$ , and this implies a contradiction to the definition of  $z_1$  and proves that (79) holds. This concludes the proof of the lemma.

Since

$$\lim_{\lambda \rightarrow \infty} \rho_c(\lambda) = e^{-\frac{c}{2}},$$

and  $\rho_c(\lambda)$  is a monotone function so that

$$0 < \rho_c(\lambda) \leq e^{-\frac{c}{2}} \quad \forall \lambda > 0,$$

we conclude from lemma 14 that

**Lemma 15.** *In the excitable case  $\beta < 0$ , we have*

$$\lambda \geq \frac{ge^{-\frac{c}{2}}}{2|\beta|} \max_{x \in \mathbb{R}} J(x) \Rightarrow \Psi(\lambda) < 1,$$

Let us note that since  $\Psi(\lambda) < 1$  implies that (52) doesn't hold, and since  $v = \frac{1}{\lambda}$ , we can reformulate the previous lemma as a lower bound for the velocities of rotating waves in the excitable case.

**Lemma 16.** *In the excitable case  $\beta < 0$ , we have the following lower bound on the velocity of any rotating wave:*

$$v > \frac{2|\beta|e^{\frac{c}{2}}}{\max_{x \in \mathbb{R}} J(x)} \frac{1}{g}.$$

The following theorem shows that, in the excitable case and for sufficiently weak synaptic coupling, there are no rotating waves (so it implies part (II)(i) of theorem 1).

**Theorem 17.** *In the excitable case  $\beta < 0$ , if  $g \in (0, g_0)$ , where*

$$g_0 = \frac{\Omega(c, \beta)}{\max_{x \in \mathbb{R}} J(x)},$$

*with  $\Omega(c, \beta)$  defined by (62), then there exists no rotating wave.*

PROOF: We shall show that if  $0 < g < g_0$  then

$$(81) \quad \Psi(\lambda) < 1$$

for all  $\lambda > 0$ , and thus that equation (52) cannot hold. By (51), (81) is equivalent to

$$(82) \quad \phi_\lambda(\pi) - \phi_\lambda(-\pi) < 2\pi.$$

We note that, by lemma 14, we already have (81) when (77) holds, hence we may assume

$$(83) \quad \lambda < \frac{g}{2|\beta|} \rho_c(\lambda) \max_{x \in \mathbb{R}} J(x).$$

We define

$$\mu = \beta + \frac{g}{2\lambda} \rho_c(\lambda) \max_{x \in \mathbb{R}} J(x),$$

and we note that (83) is equivalent to the statement that

$$(84) \quad \mu > 0.$$

Using (49) and lemma 13 we have

$$\begin{aligned} \phi'_\lambda(z) &= \lambda[h(\phi_\lambda(z)) + gR_\lambda(z)w(\phi_\lambda(z))] \\ &\leq \lambda \left[ 1 - \cos(\phi_\lambda(z)) + \left( \beta + \frac{g}{2\lambda} \rho_c(\lambda) \max_{x \in \mathbb{R}} J(x) \right) (1 + \cos(\phi_\lambda(z))) \right] \\ (85) \quad &= \lambda[(\mu + 1) + (\mu - 1) \cos(\phi_\lambda(z))]. \end{aligned}$$

which implies (note that the integral below is well-defined because of (84))

$$\int_{-\pi}^{\pi} \frac{\phi'_\lambda(z) dz}{(\mu + 1) + (\mu - 1) \cos(\phi_\lambda(z))} \leq 2\pi\lambda.$$

Making the change of variables  $\varphi = \phi_\lambda(z)$  we obtain

$$(86) \quad \int_{\phi_\lambda(-\pi)}^{\phi_\lambda(\pi)} \frac{d\varphi}{(\mu + 1) + (\mu - 1) \cos(\varphi)} \leq 2\pi\lambda.$$

If we assume, by way of contradiction, that (82) does not hold, *i.e.* that  $\phi_\lambda(\pi) - \phi_\lambda(-\pi) \geq 2\pi$ , then, using (56),

$$\int_{\phi_\lambda(-\pi)}^{\phi_\lambda(\pi)} \frac{d\varphi}{(\mu + 1) + (\mu - 1) \cos(\varphi)} \geq \int_0^{2\pi} \frac{d\varphi}{(\mu + 1) + (\mu - 1) \cos(\varphi)} = \frac{\pi}{\sqrt{\mu}},$$

so together with (86) we obtain

$$\frac{1}{\sqrt{\mu}} \leq 2\lambda,$$

which is equivalent to

$$g \geq \frac{1}{\max_{x \in \mathbb{R}} J(x)} \frac{1 - 4\beta\lambda^2}{2\lambda\rho_c(\lambda)},$$

which contradicts  $g < g_0$ . This contradiction proves (82), concluding the proof of the theorem.

We now proceed to prove that in the excitable case when the synaptic coupling is sufficiently large we have at least two rotating waves (see theorem 20 below).

**Lemma 18.** *In the excitable case  $\beta < 0$ , if there exists some  $\lambda_0 > 0$  with*

$$\Psi(\lambda_0) > 1,$$

*then there exist at least two solutions  $\lambda_1, \lambda_2$  of (52) with  $0 < \lambda_2 < \lambda_0 < \lambda_1$ , hence two rotating waves, with velocities satisfying*

$$v_1 = \frac{1}{\lambda_1} < \frac{1}{\lambda_0} < \frac{1}{\lambda_2} = v_2.$$

PROOF: By lemma 12, we can choose  $\lambda'_2 < \lambda_0$  so that  $\Psi(\lambda'_2) < 1$ . By lemma 15, if we fix

$$\lambda'_1 = \frac{ge^{-\frac{\epsilon}{2}}}{2|\beta|} \max_{x \in \mathbb{R}} J(x),$$

then  $\Psi(\lambda) < \frac{1}{\lambda}$  for all  $\lambda \geq \lambda'_1$ , and in particular it follows that  $\lambda'_1 > \lambda_0$ . We thus have

$$\lambda'_2 < \lambda_0 < \lambda'_1$$

with

$$\Psi(\lambda'_2) < 1, \quad \Psi(\lambda_0) > 1, \quad \Psi(\lambda'_1) < 1.$$

Thus by the intermediate value theorem, the equation (52) has a solution  $\lambda_2 \in (\lambda'_2, \lambda_0)$  and a solution  $\lambda_1 \in (\lambda_0, \lambda'_1)$ , corresponding to two rotating waves.

The following lemma is valid for all values of  $\beta$ :

**Lemma 19.** *Assume that  $\lambda > 0$  satisfies the inequality*

$$(87) \quad f_{c,\beta}(\lambda) < g \min_{x \in \mathbb{R}} J(x),$$

*where  $f_{c,\beta}$  is defined by (59). Then*

$$\Psi(\lambda) > 1.$$

PROOF: By (51), our claim is equivalent to

$$(88) \quad \phi_\lambda(\pi) - \phi_\lambda(-\pi) > 2\pi.$$

We define

$$\eta = \beta + \frac{g}{2\lambda} \rho_c(\lambda) \min_{x \in \mathbb{R}} J(x),$$

and we note that (87) is equivalent to

$$(89) \quad \eta > \frac{1}{4\lambda^2}.$$

Using (49) and lemma 13 we have

$$\begin{aligned} \phi'_\lambda(z) &= \lambda[h(\phi_\lambda(z)) + gR_\lambda(z)w(\phi_\lambda(z))] \\ &\geq \lambda \left[ 1 - \cos(\phi_\lambda(z)) + \left( \beta + \frac{g}{2\lambda} \rho_c(\lambda) \min_{x \in \mathbb{R}} J(x) \right) (1 + \cos(\phi_\lambda(z))) \right] \\ (90) \quad &= \lambda[(\eta + 1) + (\eta - 1) \cos(\phi_\lambda(z))], \end{aligned}$$

which implies

$$\int_{-\pi}^{\pi} \frac{\phi'_\lambda(z) dz}{(\eta + 1) + (\eta - 1) \cos(\phi_\lambda(z))} \geq 2\pi\lambda.$$

Making the change of variables  $\varphi = \phi_\lambda(z)$ , we obtain

$$(91) \quad \int_{\phi_\lambda(-\pi)}^{\phi_\lambda(\pi)} \frac{d\varphi}{(\eta + 1) + (\eta - 1) \cos(\varphi)} \geq 2\pi\lambda.$$

If we assume, by way of contradiction, that (88) does not hold, *i.e.* that  $\phi_\lambda(\pi) - \phi_\lambda(-\pi) \leq 2\pi$ , then, using (56),

$$\int_{\phi_\lambda(-\pi)}^{\phi_\lambda(\pi)} \frac{d\varphi}{(\eta + 1) + (\eta - 1) \cos(\varphi)} \leq \int_0^{2\pi} \frac{d\varphi}{(\eta + 1) + (\eta - 1) \cos(\varphi)} = \frac{\pi}{\sqrt{\eta}},$$

so together with (91) we obtain

$$\frac{1}{\sqrt{\eta}} \geq 2\lambda.$$

This contradicts (89), and this contradiction implies that (88) holds, completing our proof.

The following theorem implies part (II)(ii) of theorem 1.

**Theorem 20.** *In the excitable case  $\beta < 0$ , let*

$$(92) \quad g_1 = \frac{\Omega(c, \beta)}{\min_{x \in \mathbb{R}} J(x)},$$

*where  $\Omega(c, \beta)$  is defined by (62). Then when  $g > g_1$ , there exist at least two rotating waves. In fact, we have a ‘slow’ wave with velocity  $v_s$  bounded from above by*

$$(93) \quad v_s \leq \underline{v}_{c, \beta} \left( g \min_{x \in \mathbb{R}} J(x) \right)$$

and a ‘fast wave’ with velocity  $v_f$  bounded from below by

$$(94) \quad v_f \geq \bar{v}_{c,\beta} \left( g \min_{x \in \mathbb{R}} J(x) \right),$$

where  $\underline{v}_{c,\beta}, \bar{v}_{c,\beta}$  are the functions defined by (66).

As a consequence of (93),(94) we have, for the slow wave

$$(95) \quad v_s \leq \frac{2|\beta|e^{\frac{c}{2}}}{\min_{x \in \mathbb{R}} J(x)} \frac{1}{g} + O\left(\frac{1}{g^3}\right) \quad \text{as } g \rightarrow \infty,$$

for the fast wave in the case  $c > 0$

$$(96) \quad v_f \geq 2 \sqrt{\frac{\pi \min_{x \in \mathbb{R}} J(x)}{e^{\frac{c}{2}} - 1}} \sqrt{g} + O(1) \quad \text{as } g \rightarrow \infty,$$

and for the fast wave in the case  $c = 0$

$$(97) \quad v_f \geq 2 \min_{x \in \mathbb{R}} J(x) g + O\left(\frac{1}{g}\right) \quad \text{as } g \rightarrow \infty.$$

PROOF:  $g > g_1$  and (62) imply the existence of  $\lambda > 0$  satisfying (87), hence by lemma 19  $\Psi(\lambda) > 1$ , so that lemma 18 implies the existence of two rotating waves.

To prove (93),(94), we note that, assuming  $g > g_1$ , the range of values of  $\lambda_0$  for which (87) holds is the interval

$$\underline{\lambda}_{c,\beta}(g \min_{x \in \mathbb{R}} J(x)) < \lambda_0 < \bar{\lambda}_{c,\beta}(g \min_{x \in \mathbb{R}} J(x)),$$

where the functions  $\underline{\lambda}_{c,\beta}, \bar{\lambda}_{c,\beta}$  are defined in section 4. Thus, applying lemma 18 with

$$\lambda_0 = \bar{\lambda}_{c,\beta}(g \min_{x \in \mathbb{R}} J(x)) - \epsilon,$$

where  $\epsilon > 0$  is arbitrarily small, we obtain the existence of a solution  $\lambda_\epsilon$  of (52) with  $\lambda_\epsilon > \bar{\lambda}_{c,\beta}(g \min_{x \in \mathbb{R}} J(x)) - \epsilon$ . Since  $\epsilon > 0$  is arbitrary, we have a solution  $\lambda$  of (52) with  $\lambda \geq \bar{\lambda}_{c,\beta}(g \min_{x \in \mathbb{R}} J(x))$ , hence a rotating wave with velocity  $v_s$  satisfying (93). Similarly applying lemma 18 with  $\lambda_0 = \underline{\lambda}_{c,\beta}(g \min_{x \in \mathbb{R}} J(x)) + \epsilon$ , we obtain the existence of a wave with velocity  $v_f$  satisfying (94).

The estimates (95)-(97) follow from (93),(94) and lemma 10.

We note that along with the upper bound (95), we have a lower bound for the velocity of the slow wave, given by lemma 16.

*Question 21.* Derive an upper bound for the velocities of the fast waves (note that (94) gives a lower bound).

*Question 22.* Theorems 17 and 20 show that several of the qualitative features that we saw explicitly in the case of uniform coupling (section 4) remain valid in the general case. It is natural to ask whether more can be said, *e.g.*, whether

the following conjecture, or some weakened form of it, is true: for any  $J$ , there exists a value  $g_{crit}$  such that:

- (i) For  $g < g_{crit}$  there exist no travelling waves.
- (ii) For  $g = g_{crit}$  there exists a unique travelling wave.
- (iii) For  $g > g_{crit}$  there exist *precisely* two travelling waves.

The next theorem deals with the oscillatory case  $\beta > 0$ , as well as the borderline case  $\beta = 0$ , and in particular proves part (I) of theorem 1.

**Theorem 23.** *If  $\beta \geq 0$ , there exists a rotating wave solution for any value of  $g > 0$ , with velocity  $v$  bounded from below by*

$$(98) \quad v \geq v(g \min_{x \in \mathbb{R}} J(x)),$$

where  $v$  is the function defined by (71), and the asymptotic formulas (96), (97) hold with  $v_f$  replaced by  $v$ .

PROOF: If  $\beta > 0$ , then for any  $g > 0$  the equation

$$f_{c,\beta}(\lambda) = g \min_{x \in \mathbb{R}} J(x)$$

has the unique solution  $\lambda_{c,\beta}(g \min_{x \in \mathbb{R}} J(x))$ . Hence, any

$$\lambda_0 > \lambda_{c,\beta}(g \min_{x \in \mathbb{R}} J(x))$$

satisfies (87), so that by lemma 19  $\Psi(\lambda_0) > 1$ . On the other hand for  $\lambda$  sufficiently small we have, by lemma 12,  $\Psi(\lambda) < 1$ . Hence there exists a solution  $\lambda \in (0, \lambda_0)$  of (52). Since  $\lambda_0 > \lambda_{c,\beta}(g \min_{x \in \mathbb{R}} J(x))$  is arbitrary, we conclude that there exists a solution  $\lambda \leq \lambda_{c,\beta}(g \min_{x \in \mathbb{R}} J(x))$  of (52). Hence a rotating wave with velocity satisfying (98).

*Question 24.* Is it true that in the oscillatory case  $\beta \geq 0$  the rotating wave is always unique? We saw that this is the case when  $J \equiv 1$ .

Finally, we stress the important question of stability of the rotating waves, which remains open:

*Question 25.* Investigate the question of stability of the rotating waves, *i.e.*, do arbitrary solutions of (5), (3) approach one of the rotating waves in large time? We conjecture that, at least under some restrictions on  $J$ , the rotating wave is stable in the case  $\beta > 0$ , while in the case  $\beta < 0$  the fast rotating wave is stable and the slow one is unstable.

## REFERENCES

- [1] P.C. Bressloff, *Travelling waves and pulses in a one-dimensional network of excitable integrate-and-fire neurons*, J. Math. Biol. **40** (2000), 169-198.
- [2] G.B. Ermentrout, *Type I membranes, phase resetting curves and synchrony*, Neural Comput. **8** (1996), 979-1001.
- [3] G.B. Ermentrout & N. Kopell, *Parabolic bursting in an excitable system coupled with a slow oscillation*, SIAM J. Appl. Math. **46** (1986), 233-253.

- [4] G.B. Ermentrout & J. Rinzel, *Waves in a simple, excitable or oscillatory, reaction-diffusion model*, J. Math. Biology **11** (1981), 269-294.
- [5] F.C. Hoppensteadt & E.M. Izhikevich, 'Weakly Connected Neural Networks', Springer-Verlag (New-York), 1997.
- [6] E.M. Izhikevich, *Class 1 neural excitability, conventional synapses, weakly connected networks, and mathematical foundations of pulse-coupled models*, IEEE Trans. Neural Networks **10** (1999), 499-507.
- [7] R. Osan & B. Ermentrout, *Two dimensional synaptically generated travelling waves in a theta-neuron neuronal network*, Neurocomputing **38-40** (2001), 789-795.
- [8] R. Osan, J. Rubin & B. Ermentrout, *Regular travelling waves in a network of Theta neurons*, SIAM J. Appl. Math. **62** (2002), 1197-1221.
- [9] J.E. Rubin, *A nonlocal eigenvalue problem for the stability of a travelling wave in a neuronal medium*, Discrete & Continuous Dynamical Systems **10**, (2004), 925-940.
- [10] A.T. Winfree, 'The Geometry of Biological Time', Springer-Verlag (New-York), 2001.

EINSTEIN INSTITUTE OF MATHEMATICS, THE HEBREW UNIVERSITY OF JERUSALEM, JERUSALEM,  
91904, ISRAEL

*E-mail address:* `haggaik@wowmail.com`